XIX. *The Natural History, Anatomy, and Development of* Meloë (*continued*).

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Third Memoir.

The External Anatomy of the Larva of Meloë *in its Relation to the Laws of Development.*

Read November 2nd, 1847.

HAVING traced the natural history of *Meloë*, in the preceding Memoirs, I shall now examine its anatomy, with reference to those principles which regulate the formation of animal bodies, and which seem to be the links of connexion which associate peculiarities of instinct with the evolution, and with the functions of special structures,—commencing this with the Anatomy of the tegument.

1. *The Tegument of the young Larva.*

The tegument, the parietal tissue of the body, little important as it may *seem* to be when cursorily examined in the adult *Vertebrata*, is nevertheless, in a physiological point of view, both in the vertebrated and in the invertebrated animal, the primary and essential foundation-structure of the organized being. Like the earlier tissues of plants, it is at first composed entirely of nucleated cells. It is derived immediately from a delicate, transparent layer of semifluid cells which constitute the blastodermic envelope that is formed around one portion of the yelk shortly after the disappearance of the embryo vesicle in the ovum, subsequent to impregnation. This has already been shown in the brief outline of the course of development, and in the delineations which I have given of the ovum of that "atomic" of creation, *Stylops**; and I shall hereafter have to show that the same general laws which govern the development of that atomic existence regulate equally that of *Meloë* and of Man. This blastodermic layer of cells, folded on itself, and partially inclosing the yelk, is the structure from which the whole of the organized parts of the body concerned in the voluntary functions of the animal, are immediately derived; and, as embryologists are aware, it is to the foldings, the intus-susceptions, the extension or the shortening of portions of this structure that the primary form of the animal body is entirely due; whether it be that of the uniform and simply articulated worm, or of the rudimentary embryo of the most perfect of organized beings, Man.

The principles which thus regulate the ultimate form of the embryo that is to be, and the origination of its future limbs, ere it has any definite structural existence, regulate also the whole of its growth and metamorphoses, whether these are gradual, uniform, and uninterruptedly continuous to their end, as in most of the *Vertebrata*, or whether they are marked by more rapid and extensive evolutions at some periods than at others, as in

* Linnean Transactions, vol. xx. p. 337. t. 14. f. 23–32.

many of the *Invertebrata*, and of which the subject of our present inquiry, *Meloë*, is a striking exemplification.

It is in the tegument itself that every change of form in the external parts of the body is commenced; first in slight reduplications of this tissue to form segments; next in the aggregation or partial coalescence of these into particular sets, or regions; and lastly in the hypertrophy or excessive growth of the tegument, at definite points, which produces elevations or protrusions from the uniform surface, and which protrusions constitute the origin of the future appendages. It is by the continuation of these processes of growth in the formation of the animal,—and which processes take place by means of the enlargement and repeated fissiparous division of the nuclei of the cells of which the whole tissue is originally composed, and by the further development of these into cells, as I shall elsewhere show,—that the entire growth of the tegument, from the earliest period of its formation in the ovum to its completion in the adult animal, is effected. Portions of this tissue, consolidated by changes which ensue in the function of the nuclei of some of the layers of cells, constitute the hardened *dermo-skeleton*, which protects and gives support to the internal structures of the insect. The nuclei of these cells, instead of continuing to be multiplied by repeated subdivision into separate organisms, which in their turn are evolved into cells, seem more and more to lose their juvenescence, or reproductive power, in proportion as they are made to approach the exterior of the body by the growth of other layers of cells beneath them. They then gradually become altered in function, and the forces of growth being diminished in a ratio inverse to their maturity, earthy constituents are secreted by them in greater proportion than during their previous existence as reproductive bodies. These earthy constituents assume an inorganic, granular, or semi-crystalline form, and constitute the solid material of the hardened skeleton. This process takes place to a greater or less extent throughout the whole period of development of the insect. It commences in some parts even at an early period of the embryo in the ovum, in the solidification of the hard portions of the mandibles. It is this result of change in the function of the nuclei in their full age, and the partial aggregation of their granular contents, which lead to the deciduation of layers of the tegument in the larva. The cells with accumulated earthy matter in their interior cease to be nourished, perish, and become separated from the layers of juvenescent cells beneath them in the vigour of growth; and are ruptured and thrown off as an entire covering when they retard the further expansion of these and of the whole body. The deciduated cells do not differ, other than in these circumstances, from those which are still in the course of enlargement.

The earthy materials thus deposited in the dermo-skeleton of insects have been found by Odier*, Lassaigne†, Mr. Children‡ and others, to consist chiefly of phosphate of lime, with carbonate of potass, some carbonate of lime, and a little phosphate of iron, with, in some species, silica, magnesia and a trace of manganese. This composition led me, ten years ago§, to describe the dermo-skeleton of insects as "an imperfectly developed condition of

* Mémoires de la Société d'Hist. Nat. de Paris, tom. i.

† In Straus Durckheim's Considérations Générales sur l'Anatomie Comparée des Animaux Articulés, 4to. 1828, p. 33.

‡ Zoological Journal, vol. i. 1824, p. 115.

§ Article "Insecta," Cyclopædia of Anatomy, par. xviii. October 1839, vol. ii. p. 882.

bony matter," and as analogous in development as in function to that of the external skeleton of Chelonian reptiles. This view of its nature has recently been greatly strengthened by the discovery by Platner* of star-shaped corpuscles in the tegument of the Silkworm, very similar to those which have been described by Purkinje, Miescher, Baly†, and others in true bone.

The consolidation of the exterior tegument in insects by the deposition of earthy materials in its tissue, thus appears to be a vital process precisely homologous with that of the formation of bone in the *Vertebrata*; first by the secretion and deposition of granular, earthy, crystalline matter by the nuclei and nucleoli of cells; and next by the more complete calcification of these cells in layers which form one solid envelope. This process, deposition in layers, is recognized by the best observers, Hunter, Flourens, Goodsir, Sharpey, Tomes and others, as the mode in which the bones of *Vertebrata* are increased in diameter, through the agency of their periosteum, and not by the preparatory process of the formation and absorption of gelatinous cartilage cells, as in their first development in the fœtus. According to the experience of these physiologists, the bones of *Vertebrata* grow by the repeated deposition of layers of bony matter on their external surface, formed by the progressive calcification of layers of cells from the inner surface of the periosteum with which the bone is covered, as the woody fibre of exogenous trees is formed, by their bark. The formation and growth of new bony matter in the skeleton of *Vertebrata*, and the solidification of the tegument and of its internal processes in insects, seem thus to be results which differ in these two divisions of animals only in degree, and in the relative position of the structures in which they occur, and not in their actual nature. In the *Invertebrata*, as in the *Vertebrata*, solidification is effected by deposition in layers. The dermo-skeleton of the *Articulata* is endogenous, whilst true bone is exogenous in its mode of growth. Yet the process in both is as identical in principle as that of the formation of woody fibre in the two divisions of the vegetable kingdom. The solidification of the dermo-skeleton is carried to a greater or less extent in different parts of the body, and at different periods of the life of the insect. In the larva, when the formative energies are the most active, and the whole body is in a state of rapid growth, only the exterior layers of cells become partially calcified, by the deposition of a few earthy granules by the nuclei, exactly as the primary osseous deposits are known to take place in the *Vertebrata*. But when the growth of the body begins to be arrested, preparatory to an extensive change to the form of nymph or chrysalis, a greater number of cells become calcified, and the cast-off portion of the tegument is in consequence of greater thickness. Before the change to the perfect insect takes place, not only do more layers of cells become altered, but fibrous tissue also appears to be developed in the most internal layers, intermingled with the osteogenic; and the two, becoming firmly solidified together, thus form the insect skeleton, derived from, and inseparably connected with its dermal tissues. This perhaps may explain the cause of the inseparableness of the fibrous attachments of some of the muscles to solidified internal processes in the perfect insect, some of which, as we shall find, are formed by actual reduplications of the hardened tegument.

The whole covering of the body in the *Articulata* may thus be regarded as analogous in

* Müller's Archiv, Anat. 1844, p. 38. † Müller's Physiology, by Baly, edit. 1, vol. i. p. 379. 1837.

its mode of development, and in its function, to true bone; and even as homologous with the external bony skeleton of Chelonian reptiles; the internal portions of which are similar in structure, as in office, to the internal processes of the tegument in the *Articulata*.

But if, for the moment, in deference to the opinions of some physiologists, we were to discard this view of the nature of the tegument, and regard it simply as a dermal covering, we must still look upon it as but one structure, formed of layers of cells in different stages of growth; and not as composed of distinct tissues, epidermis, mucous layer, and corium, the definite limits of which it is perhaps impossible satisfactorily to indicate.

When a very young *Meloë* (Tab. XX. fig. 1) is examined a few days after it has left the egg, its tegument affords a complete demonstration of cellæform structure. The whole tissue, if examined under a high power, is then seen to be composed of a uniform layer of irregularly hexagonal cells (fig. 4), which are almost equally distinct in the covering of the head itself as in that of the thoracic or the abdominal segments. In some parts of the tissue, as in the more transparent ones near the spiracles (fig. 5), each cell is seen to contain a very delicate, granular, irregularly stellate nucleus, which I regard as corresponding to the cells seen by Platner in the tegument of the Silk-worm. Those cells which are on the surface of the body are of a somewhat quadrangular form, and they are arranged in a more linear direction than those which are deeper seated. Their nuclei are distinctly granulous, and occupy a very large proportion of the interior of the cells. This granular condition of the nuclei exists more especially in the cells of the thoracic segments, and closely resembles that in which, according to Mr. Tomes, true osseous matter is deposited in the *Vertebrata*. The largest of these cells measures about one two-thousandth of an inch in diameter. The cells in the tegument of the limbs are less uniform in structure than those of the body. On the femora they are slightly tuberculous, so that the limbs are a little roughened on their surface; while on the tibial and tarsal portions they are more elongated and are less distinct. This also is their condition in the antennæ (fig. 6).

The tegument has its own proper appendages in the form of hairs or imperfect spines (fig. 7). Each of these spines projects from the surface of what, at first sight, appears to be a distinct opening in the external layer, but which is an enlarged and altered cell, the size of which, sometimes, is much greater than that of the other cells, and measures nearly one thousandth of an inch. It is circular, with a convex disc, bounded by a distinct margin, and surrounded by the proper cells of the external surface. In its centre is a slight elevation, from which passes out the minute hair or spine, perfectly smooth on its sides, and gradually diminishing in size from its base to its apex. When closely examined each spine is found to be hollow from one extremity to the other. From its central origination, in a distinct structure homologous with that of the other cells of the tegument, I am induced to regard the spine, as, primarily, an excessive growth of the nucleus of a cell, everted and developed outwards as a single structure instead of being subdivided into nucleoli, or of secreting earthy matter, as in other instances, its cavity being continuous with a passage in the layers of cells beneath.

The mode in which the tegument is developed after the insect has left the egg, is similar, as I have already stated, to that of its origination in the blastoderma. I have distinctly ascertained this fact in the young *Meloë*. It commences in the formation of an

envelope around the nucleus within an adult cell, and this is followed by the fissiparous division of the nucleus itself into two bodies, which, subsequently enlarging, have each their own proper cell-wall formed around them; after which the cell-wall of the parent structure disappears, and leaves the young nuclei free to be developed into separate cells, like that from which they have originated. Thus the end of the development of a formative cell is the fissiparous division of its nucleus. This mode of development of the tegument in the young animal, after it has left the egg, is confirmatory of the theory of Schwann with reference to that of the general tissues; and it also accords with the views of Kölliker respecting the division of the yelk cells in the ovum; and with original observations made by myself, to be elsewhere demonstrated, on the mode of formation of the blastoderma.

If a transparent portion of the surface of one of the thoracic segments of a young *Meloë* which has been for some months in strong spirit, be covered with thin talc, with a little fluid around it, and be then examined by transmitted light with a magnifying power of four hundred and fifty diameters, we can immediately recognize the granular, nucleated external cells of the tegument. If then we approach the lens to the object, so as to be too near to have the external cells in focus of vision, the layer of cells beneath them is brought into view. The cells of this deeper-seated layer are smaller than those of the outer one. If the specimen examined has been several days from the egg, before immersion in spirit, then these cells, instead of having each a single granulated nucleus like those of the outer layer, are found to contain each two nuclei of equal sizes, closely approximated together, but perfectly distinct, and inclosed in one common envelope (fig. 8). In some of the cells the two nuclei are more separated than in others, while in those which have most recently changed they are closely approximated. Occasionally the original nucleus of a cell, not yet divided into two, is observed, in the commencement of its change, with a fissiparous emargination on one surface; but this fact can only be seen when the examination happens to be made on an insect in which the tegument has not far advanced in its changes. The fissiparous division of the nucleus thus appears to be the usual mode of growth of all cellæform tissues.

Although the solidified tegument supplies the place of a true skeleton in the *Articulata*, it is also the agent of other functions; which are of as much importance to the welfare of the animal physiologically, as this is anatomically. It is the medium of the transudation of effete matters from the surface of the body, the retention of which would be detrimental to the entire organism. The cellæform structure of the tegument enables us readily to understand its adaptation to this office. But, besides this, it is subservient to another function, which is equally important with that of transudation,—the aëration or oxygenation of the fluids. This is effected solely by the tegument in the very young embryo in the egg; but as the embryo is advanced to maturity, the function is shared by, and, after birth, is almost entirely performed by respiratory organs, which originate in, and are constantly connected with the tegument as spiracles, or breathing orifices in the sides of the body (fig. 1 *b b*).

These respiratory organs are among the last formed of the essential structures of the embryo. I have not been able to detect the existence of spiracles in *Meloë* until nearly

the very last period of the embryo in the ovum; since it is only in the latter periods of embryonic life, when the last portion of the yelk is inclosed in the thorax of the young insect, and when the blood has begun to be circulated, and requires to be more extensively aërated than it has already been, that organs of respiration are formed.

It is exceedingly difficult to detect the existence of spiracles in the young *Meloë* even at the moment of its leaving the egg, although formed before its escape; but at the end of a few hours, or a day, the spiracles of the trunk become distinct, although those of the abdomen are still exceedingly small. With a magnifying power of three hundred diameters they may then be seen in specimens that have been preserved in spirit. There are then *ten pairs* of spiracles (fig. 1 *b b*), *one pair* (fig. 9) in the meso-thoracic and nine pairs in the abdominal segments. They are placed on the lateral margin of the dorsal portion of the segments on each side. The first two pairs are very much the largest, and are situated, the *first* in the anterior of the mesothorax, and the *second* in the first of the abdominal segments, the fifth segment of the body. The remaining spiracles are each not more than one-third the size of the three anterior ones, and are situated in the abdominal segments, one pair in each, from the sixth to the thirteenth inclusive.

The structure of the spiracle in relation with that of the tegument, at this period, is exceedingly interesting. The two pairs of large spiracles (fig. 9) have a circular opening, with a free, smooth margin, which projects from the surface, and is bounded by the edges of the external layer of dermal cells. The orifice of the smaller abdominal spiracles (fig. 5) is at first simply an irregular oval opening, or space between three dermal cells, bounded also by a slightly projecting margin, and very similar in appearance to the stomata on the surface of the leaves of plants; thus distinctly indicating, in accordance with the views of Schleiden and Schwann, the close analogy which exists in the mode of formation of animal and vegetable tissues. The two pairs of thoracic spiracles seem to be in a more advanced stage of development than the abdominal, but in their internal condition the whole are very similar. The two anterior pairs open each into a hollow, somewhat spherical cavity, or follicle, communicating with a sinus in the granular tissue of the segment. The diameter of the cavity is about three times that of the spiracle. It is narrowed at its bottom, and there are faint indications of its further extension into the body. The follicles with which the spiracles of the abdominal segments communicate, are also much smaller than those of the thorax, and they are less clearly defined. A follicular cavity in the granular tissue of the body thus appears to constitute the *earliest* condition of the respiratory organ in the young *Meloë*, and probably also in other air-breathing *Articulata*; since these cavities in *Meloë* are precisely similar in their general appearance to those described in my former memoir in the very young *Stylops*. They also resemble in some respects the respiratory organs in *Sialis*, which, at the moment of leaving the egg, has its abdominal branchiæ filled with granulous matter, into which delicate undeveloped ramifications of the tracheæ penetrate. In *Meloë*, the parietes of the cavities are lined with an aggregation of minute embryo cells, or nuclei, of rounded shape, and similar dimensions, each one measuring about one five- or six-thousandth of an inch in diameter. Each of these embryo cells has within itself a separate nucleus. The cavity or follicle bounded by them is the commencement of the spiral-fibred trachea, the lining membrane of which, formed of these cells, is

always continuous with the external layer of the tegument, and is thrown off with it at each change. Whether the spiral fibre of the trachea, which is in the course of formation, originates, as believed by Platner, in the nuclei of cells, I am not prepared to affirm; but from the existence of nuclei in those which compose the walls of these cavities, it is probable that such may be the case.

The tegument of the head affords some peculiarities of particular interest. The cells are smaller and more uniform in size and shape than on the body and limbs, and measure each less than one two-thousandth of an inch in diameter. But those which cover the antennæ are much larger, and are as irregular as those on the legs. The eye (fig. 10), which, as formerly shown, is a single structure in this stage of *Meloë*, fitted only for near vision, has its large projecting cornea formed entirely of layers of perfectly transparent dermal cells, which are continuous with those that cover the parietes of the head, but are somewhat smaller, and measure about one three-thousandth of an inch. Those which form the circumference, and general surface of the cornea, are each slightly convex, and are all of the same size, like the corneales in the compound eye of the perfect insect*; while the centre of the cornea, the focus of the line of vision, is occupied by a single cell, much more projecting, and more than twice as large as the others. This condition of the cornea in the young *Meloë*, although perfectly distinct, is very difficult to observe, owing to the circumstance that as yet the cells constitute only portions of one nearly uniform transparent tegument of a single organ, and are not freely isolated, as is the case with the corneales in the imago. It is from this cause that these presumed embryo corneales in the larva can only be detected when the object is placed on its side, and when a high power of the microscope is employed.

This is the condition of the external portions of the tegument. When the young animal has been a few days from the egg, the deeper-seated layers of cells have in part united longitudinally, and constitute a fibro-cellæform structure, which gives attachment internally to the muscles; while the external layers continue to grow and be reproduced as distinct cells. The internal layers thus constitute the true dermo-skeleton. This may assist to explain what I have yet to demonstrate; that the organs of support which exist in the interior of the body in the perfect insect, strong bone-like processes, which give attachment to muscles, and which in some parts support and protect the nervous centres like the vertebræ in Chelonian reptiles, are solidified portions of the common tegument extended inwards, and consolidated during the metamorphoses of the insect.

Each segment of the dermo-skeleton in the imago, as shown by the late Professor Audouin†, is made up of distinct pieces, the separate development of which is but slightly indicated in the very young larva. Some of them, however, are marked in the head and thoracic segments. In the head a triangular suture is extended forwards in the middle line of the dorsal surface, between the eyes, and, diverging on either side to the antennæ, marks its line of union in the ovum. The *prothorax*, *meso-thorax*, and *metathorax*, are also marked by a median dorsal sulcus, indicating the original individuality of the two sides in the embryo, and their junction after the last parts of the yelk have been received

* See Remarks on the Origin of the Ocelli, Linn. Trans. vol. xx. p. 342.

† Annales des Sciences Naturalles (prem. série), tom. i. 1824.

into the prothorax. The dorsal region of the body in the young *Meloë*, as in the very young larvæ of most of the *Articulata*, is not so far advanced in its development as the sternal and ventral, at the period when the insect leaves the ovum; owing to its being the last portion that is formed. Consequently we find the insertions of the legs in the young, at a relatively greater distance from the median line of the sternal surface than in the imago. The legs are as it were appendages of the sides of the body; while the respiratory orifices, which properly belong to the membrane that connects the dorsal with the ventral surface in the perfect insect, actually exist in the young *Meloë* at the sides of the dorsal region. But in proportion as the growth of the body is advanced the relative dimensions and position of these parts are changed. The growth of the sternal surface, after the insect has left the ovum, does not proceed so rapidly, and is not carried to so great an extent as that of the dorsal; the result of which is that the coxæ of the legs become relatively more and more nearly approximated to the median line, and are transferred to the under surface of the body in the perfect insect. The spiracles also, from a like cause, are changed in their form and position, and are gradually removed from the dorsal to the lateral surface by the more rapid growth and extension of the former. The dorsal region itself is widened, is rendered more convex, and ultimately becomes the most voluminous portion of the whole body. These facts of development are common to all insects, and are well-indicated in the structure of the adult larva of *Meloë*, in which the entire form of the insect is completely altered by this difference in the relative development of its parts.

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2. *Tegument of the Full-grown or Pseudo-larva.*

Every natural change in the animal body, whether of structure, of function, or of instinct, takes place by regular and inevitable gradations, all of which seem to depend on immutable laws of organization. No strongly-marked transition from one condition to another, whether in character, in form, or in degree, ever occurs by sudden or violent alterations, without deranging the body, the organ, the function, or the instinct that is subject to such change, and inducing its permanent impairment, or premature annihilation.

Newton, the pride of physical science, was as fully impressed with these truths, with regard to the animal body, as with their correlatives which regulate the universe itself, when—pondering on the laws which he was then proving govern light and space—he wrote the following words:—"Idemque dici possit de uniformitate illâ, quæ est in corporibus animalium*." These views with regard to the uniformity of structure and development in organized beings,—originally glanced at by Malpighi in his anatomy of the Silkworm in 1669†, and dwelt on to some extent by our own almost forgotten countryman Dr. Willis, in 1682‡,—have since been amply demonstrated by the illustrious Geoffroy Saint Hilaire§ and his numerous followers; and it is now my humble endeavour still further to

* Optics. Edit. S. Clarke, p. 346. 4to. 1706.

† Dissertatio epistolica de Bombyce; Societati Regiæ Londini dicata. 4to. Londini, 1669.

‡ Opera Omnia. 4to. 1682.

§ Philosophie Anatomique des Monstruosités Humaines. 8vo. 1822. Also, Cours de l'Histoire Naturelle des Mammifères. 8vo. 1829.

exemplify them, together with the views of Schwann on the formation of tissues, in the Anatomy of *Meloë*, and to apply the principles on which they are based to the *functions* also of animated existence, in illustration of their dependence on special structure.

It is the great principle of gradational development which operates so markedly in the organization and habits of many of the *Articulata*, and which causes them, as we have already seen in *Stylops* and *Meloë*, to differ so greatly in every respect in their young and in their adult states. In each of these, the general conformation of body, and of each particular organ, seems to have reference to some speciality of structure or of habit; but,—owing to our imperfect knowledge,—as who will presume to say, in denial of this view, that he is cognizant of *all* the facts in the natural history of even one species of animal?—the object or applicability of every variation of structure is not always readily traceable in its *details* of colour, of armature, of size, or even in the minutiæ of form, although invariably evident in general design. We have seen this in the structure of the mandible, in the condition of the eye, in the size and power of the limbs, in the peculiarities of their tarsi (fig. 12), in the acuteness of the physical senses, and in the vivacity of the movements of the young *Meloë* in its incipient parasitism; and also like, but less needed, and consequently less marked conditions in *Stylops*. In both we have seen that gradational changes begin to be effected in the organization of the animal immediately the physical conditions in which it is placed are altered; and that these changes commence in its tegument. The *Stylops* larva, covered with its armature of spines, penetrates insidiously into the body of the Bee, and, engorged with nutritious and stimulating juices, increases rapidly in bulk, casts its embryo covering, and from an active becomes an almost quiescent being. Its elongated limbs are atrophied and reduced to mere tubercles. The spines that arm the margins of its segments,—doubtless, designed by creative Omnipotence to aid it in forcing its way into the body of the bee-larva,—as the spines on the pupa-case of the *Cossus* assist that insect in its transit to the outlet of its burrow in the trunk of the Willow, and enable it to force its way through its strong silken cocoon, preparatory to its liberation as a Moth,—then become utterly useless to the young *Stylops*, are entirely thrown off at its change of tegument. In like manner, *Meloë*, most active immediately after it has left the egg, and when designed to attach itself to the irritable Bee for conveyance to its nest, gradually becomes, after it is located and nourished there, the heavy apodal pseudo-larva. The structure of its tegument then undergoes considerable change. The forces of growth in this tissue, centred in the nuclei of its cells, and the repeated division and development of these into constituent producing portions of the whole, seem gradually to become less and less energetic at each change of tegument, the intervals of which are progressively extended. When reproduction in these constituents is long retarded, throughout the whole or chief portion of them, their arrest seems to limit the entire bulk and form of the being in that stage of its existence, and new series of changes are induced. But when growth proceeds less rapidly in some of them than in others, the form of the entire body, or of some particular region of it, is changed. The tegument of the pseudo-larva, and that which the adult larva throws off on assuming this condition, afford ample demonstration of this view. The body of the larva, altered from that of the slender, agile little being, with elongated limbs, and long caudal styles, as when it left the egg, to the heavy, fat, convex grub (fig. 13), has been changed in

its form by almost imperceptible individual differences in the development of the nuclei of the multitudes of cells of which its tegument is originally composed. The greater rapidity of growth in those of the dorsal region has occasioned the enlargement of that portion of the body to an extent far beyond that of the region which is first formed in the production of the embryo in the egg—the ventral surface—and the entire body, as a consequence, has gradually assumed a totally different outline. This primary change in one region leads to secondary changes in another, more especially in its appendages. We have an instance of this in the gradual reduction of the legs to tubercles, their enlargement, even during the feeding state of the larva, not having kept pace with that of the dorsal region; whilst at the period of change to the pseudo-larva (fig. 13), the rapid growth of this region of the body not only most powerfully arrests their further development for a time, but actually conduces to a state of atrophy, as shown in their diminished size, and in the complete deciduation of their terminal armature, the trifid prehensile claws, which we know are so important to the larva in its earliest condition. This effect of rapid growth in the dorsal region is evident not only in *Meloë* but in all larvæ that undergo similar metamorphoses, *Curculio*, *Anthophora*, *Ophion*, and other genera. It is not the result of exhaustion of the forces of growth in the undeveloped parts, but only of their retardation, the consequence of excessive development in others. In these views I refer only to the primary and essential means of development in the tissues themselves, and not to those secondary ones, which are presently to be examined, and by which the body of the insect is made to assume the imago form.

The principle which operates in the deciduation of the claws, operates equally with reference to the caudal styles (fig. 1 *d*), which have the same mode of origin as the permanent appendages of the segments, the limbs, of which they are the true homologues. The dermal appendages, spines, hairs, and scales, are similar in their *mode* of origin to the appendages of segments, but are not homologous with them. The latter always originate by an extension outwards of an entire portion of the tegument of a segment; while hairs, spines, and scales originate in the nuclei of the cells of separate layers of tegument. I have detected this origin of hairs in the embryo before it leaves the ovum. Hairs and scales are developed from the more superficial layers of cells, while spines may extend from the more deeply seated. Essentially their origin is the same. In like manner, when either cease to be nourished, their function in the economy is at an end, they become atrophied, and are thrown off with the cast portion of tegument. This is the case alike with the caudal styles and lateral hairs of *Meloë*, with the styles and marginal spines in *Stylops*, and with the enlarged branched spines on the larvæ of many *Lepidoptera*, changes which are the result of other more important ones in the organization of the animal. Function thus is the result of special structure. During the persistence of these organs they are nourished as fully as other structures, and it is only when this nourishment is diminished or withheld that they become atrophied. In many instances, as in the caudal styles of *Meloë* and *Stylops*, and the spines in *Lepidoptera*, the parts involve a large portion of the tegument, and communicate by their tubular interior with the deeper seated layers, and even with the cavity of the body, as in *Lepidoptera* and *Crustacea*. In these cases, the spine, originating apparently in a single cell in the embryo, gradually involves other cells both around and below it in its growth, until from a single part it has become

a multiple of parts, which are thrown off and reproduced like the cast tegument itself, until causes are induced which occasion its atrophy and decay. These causes rarely occur in the *Crustacea*, which do not materially change their form after the earlier periods of life. Hence the tegumentary appendages are usually retained in this Class as permanent structures: but when secondary causes of development and change of form are in operation, as in the metamorphoses of insects, then these appendages also, like the simpler dermal hairs, are deciduated. The communication of the spines, in the *Crustacea*, by their tubular cavity, with the interior surface of the tegument, as shown by a recent French observer, M. Lavalle*, proves that the spine may be an eversion and extension outwards of the whole tissue; but it does not prove, as M. Lavalle seems to think, that this is its original condition, but only that it may become this in the course of its growth as a spine. That this is the correct explanation, and that hairs, and also scales, originate primarily in the nuclei of single layers of tegument, seems proved by the fact that the skin of the full-grown larva of *Meloë* is covered in every part with extremely minute spiniform hairs, which are scarcely as much as one-thousandth of an inch in length (fig. 14). These hairs proceed each from the centre of the cells which form the layer of tegument cast by the insect on assuming the pseudo-larva state. These minute hairs are hollow at their base, like the larger ones, and are simple eversions of the nuclei of the cells of that layer of tegument; and this also is the anatomical condition of scales. That this is the fact is proved by the circumstance that not the slightest trace of these microscopic nucleus-born hairs remains in the tegument of the pseudo-larva of *Meloë*. Still further proof is derived from the facts connected with the atrophy of the spines at the last change of tegument of the larvæ of *Lepidoptera*. In these larvæ the spines, which previously communicate in their interior with the deep-seated layers of tegument, have their nourishment cut off, and their function in the economy destroyed, by the growth and enlargement of cells in their interior, extended at their base from the deeper-seated layers of tegument; so that, on the change of the larva to a chrysalis, small tubercles only remain on the tegument in places previously occupied by elongated and powerful spines.

It is in this way that not only hairs and spines, but also the armature of the distal extremities of the limbs, the claws, are thrown off, and the limbs themselves become atrophied, by deciduation of their external covering, from without inwards, as well as by actual retardation of growth: both of these results are induced to a greater or less extent in proportion as other parts or regions are enlarged.

These are some of the primary laws of the organization and growth of structure, the formation of which, thus commenced, is further advanced by secondary ones; and development is hastened or retarded by the operation of physical conditions,—light, heat, food, and all material influences.

To pass now from the *primary* stages of growth and change to the *secondary*, by which further development is effected, we must first examine the structure of the layer of tegument which the full-grown larva throws off on assuming that state in which alone I have hitherto found this insect—the *pseudo-larva*. This cast portion always partially envelopes

* Annales des Sciences Naturelles, 3me Série, 1847.

the inferior and posterior parts of the body of the pseudo-larva, thrust backwards in a packet, as it is slipped off at the period of change. In the absence of discovery of the larva itself, before it is full grown, this cast skin enables us to indicate its general form and economy, at that period of its existence, as surely as the fossil bone enables the comparative anatomist of the *Vertebrata* to indicate those of the habitant of a former world. The skin of the larva is fissured at the period of change along the median line of the prothoracic segment, and is extended forwards to the head and backwards to the meso- and meta-thoracic segments, exactly as in other insects. By carefully removing this skin from the pseudo-larva, and relaxing it in water for some hours, and then inflating it gently with a blowpipe, the general form of the larva is made apparent. It is a fat, yellow-coloured, elongated grub, with six short legs, formed of short coxal, femoral and tibial joints, covered with delicate scattered hairs, and with tarsi, each of which is a single joint, armed with a single short strong horny claw. The tarsal spines which exist in the very young *Meloë* on each side of this claw,—and which are of so much importance to the insect at that period of its existence in enabling it to cling firmly to its victim, and, relatively with other parts, are so large and conspicuous, that Léon Dufour derived from them the character of his genus *Triungulinus*,—have entirely disappeared at previous changes of the tegument. In like manner also the caudal styles have been removed, being reduced to mere pointed tubercles, as in the larva of *Cryptophagus**, preparatory to their complete obliteration in the pseudo-larva. The body is arched, slightly convex, and formed of fourteen segments, with a few scattered elongated hairs, as in the very young state; and also, as I have already mentioned, is covered on every part with multitudes of microscopic ones, scarcely one-thousandth of an inch in length, each proceeding directly from the centre of nearly every cell in this cast envelope. The segments of the body are nearly all of the same dimensions, and thus give to the larva a more uniform and less articulated appearance than that which it presents in its earliest state, when the segments of the thorax greatly preponderate.

The external organs of respiration have undergone but little change, either in form or in situation; excepting only that the second pair of spiracles are now of the same size as those of other segments. The small size of the whole, relatively to that of the body, seems to indicate a minimum degree of activity in the function of respiration, and consequently a sluggish mode of life, similar to that of the Bee-larva, in the abode of which the *Meloë* is a parasite. The spiracles at this period are not larger than those of the Bee-larva, excepting the anterior pair. The whole are nearly circular in form, and their entrance is protected by a raised horny margin. Internally they are lined by a membrane made up of extremely minute but distinct cells, which form a layer that is continuous with the mucous lining of the trachea. This lining is removed in connexion with the cast skin from the whole of the ramifications of trachcæ connected with each spiracle; and its delicate, hair-like, tubular, uniform divisions, which pass off from the main stems at acute angles, further prove that the capacity of the tracheæ, and consequently their function as respiratory organs, is insignificant and restricted.

This cast envelope of the full-grown larva shows that, up to this time, the head has

* Linn. Trans. vol. xx. p. 352. tab. 14. fig. 34.

undergone but little alteration in form from that of the very young, like which it is marked with a longitudinal and a triangular sulcus. The eye, which in the embryo larva is a single organ, is now a compound one, formed of three facets on each side of the head. In this multiplication of parts it resembles the eye in the lower *Myriapoda*, the *Julidæ*, in which the eye, commencing as a single structure, becomes at its first change a triple one*, preparatory to future subdivision to form the compound eye of the imago. Up to this period the antenna has undergone less change than any other structure of the head, thus proving that, whatever is its function, it is exercised in precisely the same manner in the adult as in the very young larva. But it is in the parts of the mouth that the greatest changes of form have occurred; changes which lead us to infer a change in its economy. The *mandible* of the adult larva, as I have formerly stated, is a short strong corneous organ, totally different from that of the embryo larva. It is in this that the mode of development by anchylosis, or complete union of originally separate parts, in the formation of one structure or body, is most distinctly shown. The mandible in the original formation of the embryo in the egg is the true and legitimate appendage of, at least, one of the basilar segments of which the entire head is composed, and which segment is identical in its mode of origin with the other segments of the body. This fact I had the honour of announcing in the 'Transactions' of this Society, as discovered in the embryo of *Geophilus*†; and although it has been somewhat questioned by Prof. Erichson‡, I have since been enabled to verify it repeatedly, not only in the *Myriapoda*, but also in the embryos of true insects—for example, in *Forficula*. To trace the formation of the mandible, therefore, we must regard it as the articulated appendage of a single segment,—in fact, a true limb in its origin and structure, but which, gradually altered in its condition and form, becomes adapted to a particular function, and to variations in the mode of its employment in that function. The changes in this structure usually take place in animals at so early a period, often, as in the whole of the *Vertebrata*, even during the earliest stages of the embryo, that we are unable to follow them, and satisfy ourselves of the fact of their occurrence. But this is not the case in the lower forms of *Articulata*, the *Myriapoda*, nor even in *Meloë* and many other hexapods. In the embryo of the vermiform *Myriapoda*, as in *Geophilus*, every segment of the body is furnished with a pair of appendages, and this also is the case with each of the segments of the head. These appendages originate at the sides of each segment as minute tubercles, one pair to each. Those which belong to the head appear first, but are followed in quick succession by those of the anterior segments of the body, and sooner in proportion to their proximity to the head. No difference is at first recognizable in any of them, either in form or size; but after a period more or less brief, according to the type and species of animal, the mandible becomes enlarged and changed in its appearance. In the *Chilopodous Myriapoda* it retains the articulated pediform structure throughout the entire life of the animal, and is employed as an organ of prehension rather than of manducation. This is precisely what we have already seen in the very young *Meloë*, which has a mandible jointed and pediform in structure, and penetrant and prehensile in function. The structure of an organ thus indi-

* Phil. Trans. 1841, p. 127. † Linn. Trans. vol. xix. p. 289.

‡ Reports on Zoology for 1843–44 (printed by the Ray Society); Entomology, by Dr. W. F. Erichson, p. 409.

cates the purpose for which it is employed; and the habits of the *Meloë* larva, and its mode of seizing and attempting to pierce the skin of the bee that conveys it to its nest, confirm the conclusion deduced from the structure of its mandible.

The gradual change of form which the mandible undergoes in the larva state, indicates some modification of function even during the larva period. I have already shown that the mandible in the adult larva is a short thickened corneous organ, more nearly resembling that of the perfect insect: not as in that fitted for cutting and comminuting vegetable tissue, nor, as in the very young, for piercing soft textures, but rather adapted for crushing and bruising. The mode in which this organ is changed in its condition is, first, by deciduation, at the change of tegument, of its terminal claw-like apex, exactly as the corresponding part of a true limb is thrown off at the change on the reduction of the legs to mere tubercles, preparatory to their future re-development in the nymph or pupa in a new form; next, by the growth and enlargement of every part of the structure in a *lateral*, and its retardation in an *axial* direction. The result of this change is a complete obliteration and anchylosis, or permanent union of the whole in one powerful angulated structure, which retains an articulation only with its parent segment. This is the mandible of the adult larva.

Changes, similar in principle and mode of operation, but carried to a far less extent, take place in the other appendages of the cephalic segments of *Meloë*, the maxillæ and palpi, the function of which, like the structure, undergoes but little modification.

The whole of the feeding-period of the larva state, in so far as refers to change in the segments of the body, is scarcely other than one of simple growth and enlargement. Change of form by aggregative development, as we have seen, commences in the appendages and parts of the head; but the tegument of the segments in the larva still retains its original flexible uniform condition, and is scarcely thrown into folds, even at the junction of separate segments. The nuclei of its component cells continue to reproduce, and when the external layer becomes aged and resistant, obstructing the function of the internal, it ceases to be nourished and is removed. But as the entire body advances to its maximum of size, certain forces become active in its internal structures, which lead to those rapid and important changes of form in the whole which we recognise as the *Metamorphoses of the Insect.*

Those structures which are the immediate agents of all voluntary and instinctive movements, *the muscles*, are also those of the Metamorphoses. Nourished to the utmost while the larva is feeding, they keep pace with the tegument in growth. They are connected with the internal surface of the tegument in every part of the body, deriving their origins from it, and having their attachments in it; so that any alteration in them affects the form of the portion they are connected with, and of the whole body, to a greater or less extent in proportion to the degree of their contractility, and to the number and direction of the muscles engaged.

We are entirely ignorant of the secret cause which first excites these structures into action in effecting the metamorphoses, at definite periods of the insect's existence, if it be not, as there seems reason to suspect it is, allied to an accumulation, and subsequent discharge, of force evolved during growth in the structures themselves, a vital endowment of

organized matter: we only know, of a certainty, that it is by the agency of the contractile muscles that the form of the body is rapidly altered at the period of metamorphosis, and that whatever is the origin or the nature of the contractile power, its evolution is accelerated or retarded by physical influences. Alternations of heat and cold, drought and moisture, are favourable to the changes which this power effects, and promote their occurrence, as an unaltered continuance of either of the conditions mentioned retards them. Reaumur found that by keeping chrysalids of the common white butterfly in an ice-house, the changes to the perfect insect were prevented for two years; whilst by removing others in the depth of winter to a hot-house, he induced the appearance of the perfect insects in a few days. I have myself noticed similar facts in the *Hymenoptera*. Some larvæ of *Anthophora*, which I collected in the month of October, and preserved in a warm room through the winter, instead of undergoing transformation, as in their natural haunts, on the accession of warmth, in February and March, did not change into nymphs until some hot days in August, when the temperature of the apartment was greatly increased; and having entered the imago state in a few days afterwards, then lapsed into perfect quiescence, or sleep, as in their natural state of hybernation, and did not become active until the following spring *. Thus alternations of condition are essential to the changes in growth and development, as to the health of the body, and to the evolution of all vital power. This is equally true with reference to the highest, as to the lowest of created beings; to the most perfect, as to the least organized; to ourselves, as to the insect we are examining.

Influenced by alternations of condition in the functions of respiration and nutrition, the muscles of the insect acquire an accumulation of contractile power before the change; and when the larva has attained its full size, and its further growth is arrested, the moment of transformation has arrived, and this power in the muscles constitutes the *secondary* and most evident means of development. Certain muscles in the insect are ranged in the axis of its body, in a longitudinal direction, attached to the internal surface of the tegument in parallel series at the anterior margin of one segment, and extended to the posterior of another; and others are ranged in diagonal, or in transverse series. By the action of the longitudinal ones, aided by the diagonal, and operating on the whole structure, the main portion of the tegument is gradually separated from the worn-out external layer that is to be removed; and by a concentration as it were of the muscular forces in the segments immediately behind the head, this layer is ruptured along the dorsal surface; and, gradually detached from the new covering beneath it, it is slipped off backwards by successive contractions and elongations of the segments.

When this change takes place after the insect has acquired its full growth as a larva,

* Since this paper was read I have repeated this observation. Some specimens of *Anthophora* obtained in the larva state on the 12th of September 1847, were preserved in a room of moderate temperature during the winter; but they did not change to nymphs until from the 7th to the 14th of July 1848, and then only assumed the perfect state in September of the same year; after which they did not throw off the last tegument until January 1849, and became active imagos in February. I pointed out this fact of arrested development, at a uniform high temperature, at a Meeting of the Entomological Society in April 1847. (See Trans. Ent. Soc. vol. v. pt. 2, 1847, p. xi.) I may mention also that five of the larvæ which were the subjects of this experiment, were of a deep *yellow* instead of a *white* colour, and that two of them produced male, and three female imagos, so that difference of colour has no reference to the sex of the individuals.

and has ceased to feed, as at the period at which I have found the full-grown *Meloë*, the museles effeet a complete alteration in the segments both relatively and individually. The abdominal segments, which are the largest while the larva is feeding, are quickly reduced in size when fresh nourishment has ceased to be supplied; while those of the thorax are enlarged, and duplicatures of tegument are formed between each by the shortening of the longitudinal and diagonal muscles.

In the pseudo-larva of *Meloë* (fig. 13) these changes have only commenced; but when the insect passes to the nymph or pupa state (fig. 15), the alteration is carried to a very great extent. The longitudinal muscles of the abdominal segments occasion, by their powerful contraction, broad reduplications of the tegument, the posterior margin of one segment is made to cover the anterior of the one next behind it, and the whole are much shortened. The force of development in this region is from behind forwards, the effect of which is to occasion a rapid enlargement of the head and of the thoracic segments, and the coalescence of some of the latter by aggregation and anchylosis. This is carried to the greatest extent in the segments of the middle of the body, which form the union of the thorax and abdomen in the imago. In some insects the fifth segment of the larva is reduced to its minimum, and disappears as a sectional portion of the animal, its rudiments only being left. In the nymph or pupa of *Meloë* the metathoracic or fourth segment is the shortest, the fifth being further shortened at the next change.

The immediate result of the altered proportions of the abdominal segments, and their removal forwards by the action of the museles on the tegument, is a re-induction of the forces of growth in the appendages of the thoracic and cephalic segments, and a consequent enlargement of the segments themselves, more especially those of the head. This region in *Meloë* is enormously enlarged, as compared with the head of the larva. But this does not result, as M. Ratzeburg seems to think, from certain observations he has made on *Hymenoptera*, from a coalescence of the head of the larva with the segment next behind it, but it is entirely due to the rapid growth and expansion of all parts of the head at the period of transformation.

The change effected while the larva is passing to the pseudo-larva state, is a commencement of a re-induction of the growth of the appendages of the head and thorax. The legs, then reduced to tubercles, are soon redeveloped beneath the tegument of the pseudo-larva in an entirely new form, with jointed tarsi, ready to be elongated at the instant of change to the nymph.

In addition to the redevelopment of these parts, the rudiments of new organs are produced. The internal respiratory structures are extensively affected by the changes, as is the case in all insects on becoming pupæ, and the result is to occasion the expansion of a fold of the tegument, at the sides of the metathorax (fig. 16 *a*), in which some ramifications of tracheæ are included. The growth of this fold in *Meloë* is soon arrested, and it becomes the future rudimentary elytron of the imago, as in other insects it is the anterior wing.

Minor causes, which it is unnecessary to mention here, not only occasion these parts to be developed to a greater extent in some species than in others, but also effect the production of a second fold from the metathorax, the posterior wing.

Besides these there are other important changes in the tegument in these transforma-

tions, changes which constitute it the true skeleton of the insect. The alterations which the body undergoes in form are not accidental results of the actions of the muscles, *but depend in each species on definite unvarying geometrical principles of force and relation.* Portions of the tegument which give attachment to muscles are folded inwards in the head and thorax, and becoming solidified constitute a rudimentary internal skeleton, some parts of which merely give attachment to muscles, whilst others, as in the *Vertebrata,* inclose and protect the nervous system. These I shall hereafter examine with the *dermo-skeleton* of the imago.

EXPLANATION OF THE PLATE.

Tab. XX.

Fig. 1. The young *Meloë* a few days after it has left the egg, highly magnified to show the structure of the organs of vision, *a*; situation of the spiracles, *b*, *b*; form of the tarsi, *c*, *c*, and caudal styles, *d*; and internal muscular structure as seen by transmitted light.

Fig. 2. Inferior surface of the *Meloë* larva, showing the structure of the pectoral and abdominal portion of the tegument.

Fig. 3. *Meloë* larva seen from above by transmitted light, and showing its brain and alimentary canal.

Fig. 4. A portion of the tegument highly magnified, showing its hexagonal cellæform structure.

Fig. 5. One of the abdominal spiracles magnified, showing the tegumentary cells with irregular granular nuclei.

Fig. 6. One of the antennæ, highly magnified.

Fig. 7. A dermal spine or hair, originating from the nucleus of a single cell, highly magnified.

Fig. 8. Portion of tegument showing two layers of cells, the deeper-seated with their nuclei divided and in the course of reproduction.

Fig. 9. The large or thoracic spiracles.

Fig. 10. The eye of the larva, magnified, showing the cornea formed of tegumentary cells, with the single central ocellus.

Fig. 11. View of the side of the head of the larva.

Fig. 12. One of the tarsi, showing the articulated spines at the sides of the true claw.

Fig. 13. The full-grown or pseudo-larva, with its limbs reduced to tubercles preparatory to change to a nymph.

Fig. 14. Skin of the full-grown larva, showing the microscopic hairs developed from the nuclei of cells.

Fig. 15. The nymph at the period of throwing off the pseudo-larva covering, with its limbs becoming rapidly enlarged.

Fig. 16. The fully-formed nymph.